possible a repetition of the Morrill land grant to the states; but it would be possible to issue 5% bonds which benefactors of higher education could buy for the support of graduate work in a special institution. By making these bonds inalienable a permanent fund would be established. The low ruling rate of interest would thus make the matter a genuine piece of coöperation on the part of the government, and in so far as the 5% exceeds that rate there would be a government grant.

It is, then, to emphasize the fact that the most recent thought concerning the formation of a national university does not contemplate flooding the District of Columbia with a body of untrained or partly trained students that this letter is written. It is desired that the government foster research, establishing a national university with branches, providing in the central establishment broader opportunity for research, increasing in the state branches the facilities for training graduate students.

SUSANNA PHELPS GAGE.

ITHACA, N. Y., February 9.

GASKELL'S THEORY OF THE ORIGIN OF VERTEBRATES FROM CRUSTACEAN ANCESTORS.

To the Editor of the *American Naturalist:*

SIR, — Since the Annelid theory of the origin of vertebrates, at one time so generally and enthusiastically advocated, has failed to realize the expectations of its adherents, interest in the subject has steadily fallen off, and the various attempts to substitute something in its place have gained only individual or, at most, a very small number of followers.

The impression has steadily gained ground that in spite of its very great importance the problem of the origin of vertebrates is no longer a fruitful one for discussion, because the evidence accessible is so general in character that one may make out a reasonable theory based on almost any invertebrate that one may be pleased to select. We believe, however, that there is no reasonable justification for this state of mind, and that perhaps it may be in a measure overcome by showing how any radical departure from certain lines of procedure, even if the utmost liberty is exercised in the destroying of old organs and the creation of new ones, fails to make the solu-

tion of this problem any easier, and in the end leads to hopeless confusion. It will, therefore, be interesting and profitable to consider some of the difficulties into which Mr. Gaskell is led in his attempts to solve this problem by the novel method of comparing the dorsal surface of an arthropod with the dorsal surface of a vertebrate.

It may be stated incidentally that Mr. Gaskell adopts, without acknowledgment, the same lines of argument in reference to many homologies between vertebrates and arthropods that were used in my first paper on this subject in the *Quarterly Journal.* This is notably the case in regard to the paleontological evidence, the relation of the endosternite of arachnids to the cartilaginous cranium of vertebrates, and to the causes for the disappearance of the old mouth in the concentration of the thoracic neuromeres around the arachnid œsophagus, although these facts are quite inapplicable to his theory..

Briefly stated, Gaskell maintains (*Journ. of Physiol.*, 1889, p. 191) that the nervous system of vertebrates is composed of two essentially different parts: first, a preëxisting, non-nervous tube, consisting of the epithelium of the canalis centralis and cerebral vesicles, and the various supporting elements derived from it; and, second, the true nervous elements, consisting of a "bilateral chain of ganglia connected together by means of longitudinal and transverse commissures." The infolding of the medullary plate of vertebrates shows us, he maintains, the simultaneous development of two different organs, the one the nervous system, and the other the tube of supporting tissue, p. 193. This tube of supporting tissue, "which is not nervous and never was nervous," and which is coextensive with the canalis centralis and the cerebral ventricles, Gaskell regards as the remnants of the alimentary canal of a crustacean-like ancestor. The ventral cord and the supraœsophageal ganglia of the crustacean ancestor have in vertebrates fused with and grown around the old alimentary canal to form the true nervous elements of the spinal cord and brain. *No reversal of surfaces is called for by this transformation*, for the ventral surface of an arthropod is regarded as homologous with the ventral side of a vertebrate. . . . He maintains that the one reason why they (the champions of the origin of vertebrates from the appendiculata) have not been able to make any real advance in their views, has been the difficulty of accounting for the altered relations of alimentary canal and nervous system in the two groups. His theory "solves this difficulty,"

not by turning the animal over, but by transporting bodily the crustacean nerve cords and alimentary canal from the ventral to the dorsal side. By this simple process everything of importance that happens to lie between the dorsal and ventral surfaces must be either swept out of existence or forced into some corner where it undergoes extensive and complete degeneration. The result is a metamorphosis so profound that morphologists have completely failed to recognize the organs of the crab in their new forms and places. According to Gaskell, during the transition from crustacea to vertebrates, the crab's heart is nearly crowded out through the back by

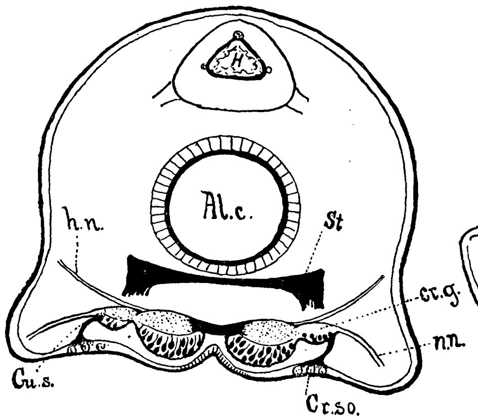

FIG. 1.

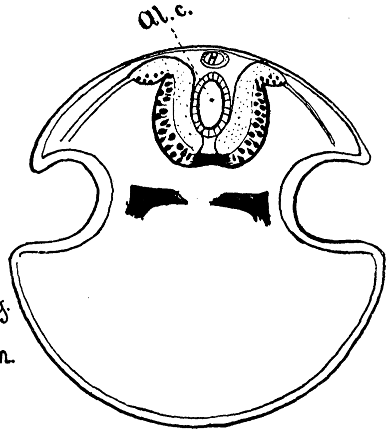

FIG. 2.

FIG. 1. — Diagrammatic cross-section of an arachnid (Limulus) in the head region, showing the relative position of heart, alimentary canal, endosternite, and principal peripheral nerves and commissures.

FIG. 2. — Cross-section of a vertebrate illustrating Mr. Gaskell's theory that the arthropod nerve cords, alimentary canal, and endosternite have been transferred to the original dorsal surface where the heart and alimentary canal undergo extensive degeneration.

the dorsal movement of the nerve cords, although it still lingers in Ammocœtes, where he has detected it as "that peculiar elongated organ, composed of fattily degenerated tissue, which lies between the spinal cord and the dorsal median skin." It is not clear whether it was the peculiar elongation of the organ or the presence of fat in it that enabled him to recognize the heart of Limulus in such an unusual place. Gaskell also proves, in the same manner, that the nephridia, or coxal glands of arthropods, have been disguised as the pituitary body of vertebrates; the genital part of the opercular appendages, as the thyroid glands and pseudo-branchial groove; and he shows how the gigantic liver of crustacea is reduced to a mass

of "sub-arachnoidal glandular tissues," that helps fill up the cranial cavity, and thus keeps the brain in place. The straight intestine is discovered under the guise of the central canal of the spinal cord and the "cephalic stomach" as the ventricular cavities of the brain. These are only a few of the renovations to which the crabs must submit in their efforts to become vertebrates. There is not much left that can be used to advantage in the "new crab," except the skin and bones, and Gaskell makes a good deal of them, although he does not display as much ingenuity in doing so as in some of the instances quoted above, because the essential points of resemblance between the cartilages and the dermal structures of Limulus and those of vertebrates have already been pointed out by the author. Gaskell hopes to explain some time how our eviscerated ancestors acquired a new heart, kidneys, and productive organs, as well as a new alimentary canal complete, from mouth to anus.

Gaskell argues that he is justified in "violating the embryological unities," as he calls them, on the grounds that there is much scepticism abroad concerning the validity of the germ layer theory. But this weakness of the germ layer theory can hardly be construed as a license to transfer a crab's entire alimentary canal and nervous system from the ventral to the dorsal surface without obtaining some authority from established facts, yet the assumption that this transfer has taken place forms the foundation of Gaskell's theory. The conception is untenable, not because the supposed transfer of organs is a novel and surprising one, or because it is difficult to see how the animal could survive the operation, but because it assumes a condition of affairs that does not exist, because the peripheral nerves and the cross commissures present impassable barriers to the proposed changes, and because the suggestion is inconsistent with the most obvious facts of embryology.

In 1896 (*Nature*), about eight years after the idea first occurred to him, Professor Gaskell is led to suspect that there may be some difficulties in homologizing the hæmal surface of a crab with the neural surface of a vertebrate, and gives the following explanation:

The ontogenetic test appears to fail in two points:

(1) "That the nerve tube of vertebrates is an epiblastic tube, whereas, if it represented the old invertebrate gut, it ought to be largely hypoblastic.

(2) "The nerve tube of vertebrates is formed from the dorsal surface of the embryo, while the central nervous system of arthropods is formed from the ventral surface.

"With respect to the first objection, it might be argued, with a good deal of plausibility, that the term 'hypoblast' is used to denote that surface which is known by its later development to form the alimentary canal, that in fact, as Heymons has pointed out, the theory of the germinal layers is not sufficiently well established to give it any phylogenetic value." Are we to understand from this that since the canalis centralis does not develop into an alimentary canal, it is probably hypoblastic?

"The second objection appears to me more apparent than real. The nerve layer in the vertebrate, as soon as it can be distinguished, is always found to lie ventrally to the layer of epiblast which forms the

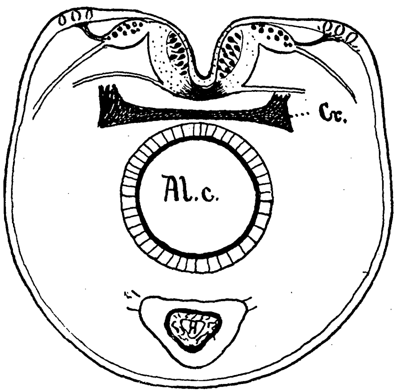

FIG. 3.

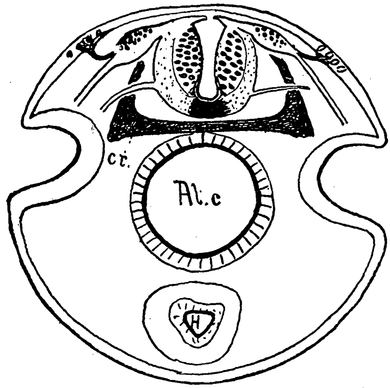

FIG. 4.

FIGS. 3, 4. — Cross-sections of a vertebrate in the head region, illustrating how the vertebrate condition may be attained by turning the arthropod over on to its dorsal surface, thus bringing its principal organs into the same relative position as in vertebrates. No degeneration of old organs or formation of new ones is required according to this view. The epithelium of the canalis centralis and ventricles thus appear not as parts of an old alimentary canal, but as the infolded ectoderm that from the first overlies the brain and spinal cord, and from which they are phylogenetically as well as ontogenetically derived.

central canal. . . . The nerve layer in the arthropod lies between the ventral epiblast and the gut; the nerve layer in the vertebrate lies between the so-called hypoblast (*i.e.*, the ventral epiblast of the arthropod) and the neural canal (*i.e.*, the old gut of the arthropod). The new ventral surface of the vertebrate in the head region is not formed until the head fold is completed. Before this time, when we watch the vertebrate embryo lying on the yolk, with its nervous system, central canal, and lateral plates of the mesoblast, we are watching the embryonic representation of the original Limulus-like animal; when the lateral plates of the mesoblast have grown round,

and met in the middle line to assist in forming the new ventral surface, and the head fold is completed, we are watching the embryonic representation of the transformation of the Limulus-like animal into the scorpion-like ancestor of the vertebrates."

It is not quite clear what Mr. Gaskell means by the above statement, but if I understand him correctly, it is clear that if the embryonic shield of a vertebrate embryo represents an arthropod embryo on the old arthropod hæmal surface, then the growing margins of the mesodermic area must lie *between* the nerve cords, and they should grow toward the mid-dorsal line and concresce there. But nothing of the kind is to be seen in vertebrates, because the mesoderm lies mainly *lateral* to the nerve cords, and grows in the opposite direction to what it should according to Gaskell's theory, namely, toward the vertebrates' true hæmal surface. Moreover, the transformation of the "Limulus-like animal into the scorpion-like ancestor" should show us not merely the growth of the mesodermic plates, but the migration of the canalis centralis and the nerve cords from their first position in the embryonic shield of a vertebrate (*i.e.*, the Limulus condition) to the opposite side of the egg, *i.e.*, the vertebrate position. But the nerve cords and canalis centralis are already in their permanent vertebrate position, and for that very reason, according to his own supposition, they cannot also be in the Limulus position! The reader may perhaps doubt whether Gaskell, in his earlier papers, thought that the alimentary canal of arthropods arose from the dorsal or the ventral surface of the egg. If he supposed it arose from the ventral surface between the nerve cords, then how can it appear in vertebrates at the very outset of development at the opposite side of the egg? Consultation of the text leads one to suspect that the difficulty is to be solved by taking the entire roof off the crab, leaving nothing but the ventral surface behind, for he also claims that in vertebrates the infolding of the medullary plate represents the simultaneous development of the nerve cords and alimentary canal of the ancestral crab, hence they must appear on what was the ancestral ventral side, so that we must suppose the medullary plate of vertebrates is seen through an imaginary dorsal portion of the ancestral crab, like the coat-tail buttons on the back of Marley's ghost; or, if he wishes to avoid this dilemma by an appeal to the tottering theory of concrescence, he will be forced to look on the vertebrate blastopore not as the original mouth of a remote ancestor, but as the entire dorsal surface and sides of a crab, into which are gradually swept all the organs which, in a crustacean, lie dorsal to the nerve cords and

alimentary canal. If Mr. Gaskell accepts this alternative, he will find it difficult to explain how the alimentary canal of the ancestral crab was split into two surface cords of cells that sweep round to the opposite side of the ovum to form the canalis centralis of vertebrates.

Gaskell bases his comparison of the pineal eye of vertebrates with the ocelli of arthropods mainly on their minute structure, neglecting their mode of development and the fact that there are two distinct types of arthropod ocelli, namely, the paired ocelli, with upright retinas, as in Dytiscus and Hydrophilus, and the ocelli with inverted retinas, formed by the fusion in the median line of two or more ocelli (*e.g.*, median ocelli of scorpions, Limulus, and possibly some crustacea). As we have shown elsewhere, the latter are the only ocelli that can be compared with the pineal eye of vertebrates, both on account of their position and the fact that they are the only ocelli which lie at the end of tube-like outgrowths from the roof of a cerebral vesicle. This condition is brought about in scorpions and in Limulus by the overgrowth of a lateral fold of ectoderm, which in the scorpion completely encloses the cephalic lobes or forebrain, leaving the inverted ocelli at the end of a tubular outgrowth of the roof of the vesicle. This is one of the most satisfactory indications we have of a relation between vertebrates and arthropods, for it shows us in detail how the eyes of vertebrates have in all probability been inverted and transferred from the lateral edges of the cephalic plate to the ends of tubular outgrowths of a cerebral vesicle. In Gaskell's earlier paper (*Quart. Journ.* p. 50, 1889) he compares the pineal eye of vertebrates with the ocelli of Dytiscus and Hydrophilus. He then constructs a diagram of the vertebrate pineal eye, which is almost an exact copy of the ocelli of Dytiscus, and this diagram is printed in three colors, to show that the pineal eye of vertebrates "is clearly that of an arthropod, and indeed of an ancient form" (p. 53, 1889). As a matter of fact, however, the ocelli of Dytiscus and the pineal eye of vertebrates are not in the least alike, and the mode of development in the two cases is entirely different. On the other hand, the median ocelli of scorpions and of Limulus do resemble in a most striking way, in their position and development, the pineal eye of vertebrates. These ocelli *already lie at the end of a tubular outgrowth from the roof of a forebrain vesicle.* These facts perhaps escaped Gaskell's attention, although they were described in the same number of the *Quarterly Journal* as his earlier paper. They are fatal to his view that the forebrain vesicle is a remnant of an arthropod alimen-

tary canal, because if the arthropod brain is already hollow, why should any one introduce the alimentary canal into it in order to explain why the brain is hollow in vertebrates?

I have described in the same number of the *Quarterly Journal* in which Gaskell's earlier paper appeared how the cartilaginous endosternite in scorpion and Limulus is comparable in shape and in its relations to the brain and alimentary canal with the primordial cranium of vertebrates, and how a complete ring is formed about the posterior part of the brain, like the occipital ring seen in the early stages of

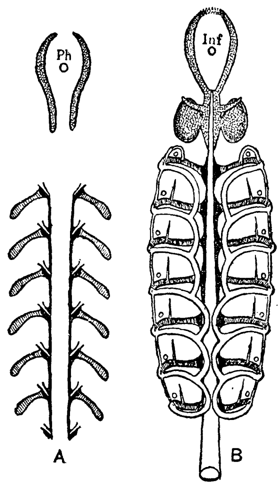

FIG. 5. — Gaskell's diagrams of the cartilages constructed by him to show how much the cartilaginous skeleton of Limulus, A, resembles that of Ammocœtes, B.

the cartilaginous cranium of vertebrates. Gaskell makes no reference to these facts, but nevertheless he lays great stress on the presence of the endosternite, although it lies on the opposite side of both the nervous system and the alimentary canal from what his theory demands. To meet the requirements of his theory, the endosternite must first be split in halves lengthwise, and the two parts transferred to the opposite side of the nervous system, and then, after their reunion, a new occipital ring must be formed on the opposite side of the sternite from the one where it actually is formed in the arachnids. (Compare Figs. 1 and 2.) And before all these changes could take place, the long fragments of the sternite would have to plough their way through the nervous system, beneath the epithelium of the cerebral vesicles and the canalis centralis (Fig. 1). But even then,

to get entirely out of the trap, they would have to break through either all the cranial nerves, if they passed out laterally to the nerve cords, or else all the cranial cross commissures, if they passed between them.

In order to make the similarity between the cartilages of Ammocœtes and those of Limulus more apparent, Gaskell produces two

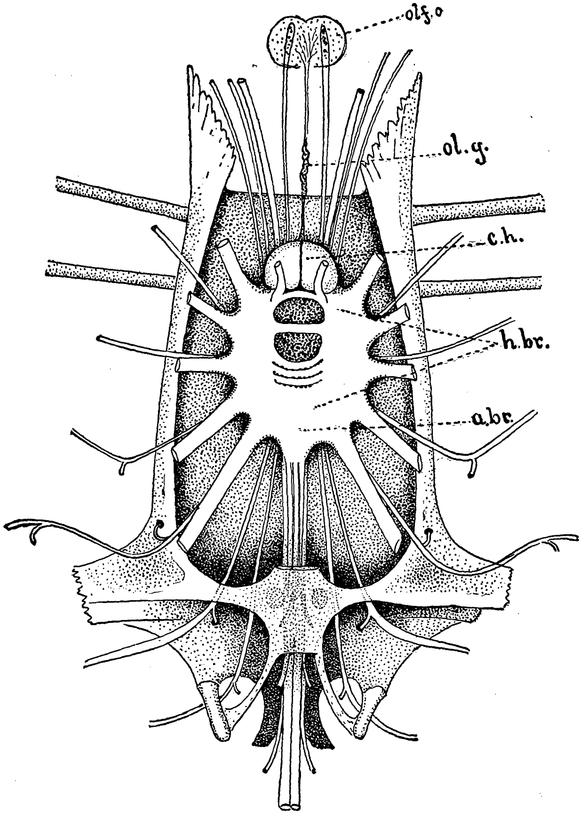

FIG. 6. — The endosternite of Limulus seen from the ventral side, with the brain and anterior part of the spinal cord in place, about natural size. The posterior part of the cranium is roofed over by a tough membrane, which on the sides gradually changes to the cartilaginous arches that help form the occipital ring, through which pass the spinal cord and several pairs of nerves. The sides of the cranium are perforated by two pairs of foramina, through which pass branches of the hæmal nerves. This cartilage is represented in Gaskell's diagram by the two bow-shaped cartilages on either side of *Ph.*

diagrams side by side (*Journal of Anatomy and Physiology*, Vol. XXXII, p. 556). One is a diagram of the cartilaginous skeleton of Ammocœtes, the other is labeled a "diagram of the cartilaginous

skeleton of Limulus" (Fig. 5 A). The diagrams do resemble each other very much no doubt, but the Limulus diagram can hardly be regarded as an accurate representation of the cartilages of that animal, as may be seen by comparing it with a drawing made directly from the object itself (Fig. 6). This figure is copied from one in a paper about to be published by Mr. Redenbaugh and myself, on the cartilages of Limulus, Apus, and Mygale. It is not easy to account for the construction of Mr. Gaskell's extraordinary diagram, since the endosternite of an adult Limulus is, roughly, two inches wide by three inches long, and several millimeters in thickness, a single heavy plate of tough cartilage, not readily broken or distorted. It has, moreover, been repeatedly figured and described, and Gaskell has himself dissected it and studied its histological characters.

Papers like the ones we have just reviewed are unfortunate. They are not a credit to the science of comparative morphology, and the interest in the whole subject of the origin of vertebrates suffers from the reaction induced by such efforts.

WILLIAM PATTEN.

HANOVER, N. H.